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AGE AND FORAGING ABILITY RELATIONSHIPS OF OLIVACEOUS CORMORANTS

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The gradual development of food capturing abilities by young birds has been documented in several species that exhibit marked differences in foraging methods and sites. The young of Brown Pelicans (*Pelecanus occidentalis*; Orians 1969), Little Blue Herons (*Florida caerulea*; Recher and Recher 1969), Sandwich Terns (*Sterna sandvicensis*; Dunn 1972), and Adelie Penguins (*Pygoscelis adeliae*; Ainley and Schlatter 1972) all capture prey less successfully than do adults of their species. Although immature Royal Terns (*Sterna maxima*) capture prey as successfully as adults, they must increase feeding time due to slower diving rates (Buckley and Buckley 1974).

Relative foraging inefficiency by immatures has been given as a primary reason for evolution of delayed breeding in birds. Lack (1954, 1966, 1968) and Ashmole (1963) developed the basic premise that an individual's chances of surviving and producing offspring increase by delaying first reproduction until some optimal time as determined by local conditions.

Most cormorants normally exhibit a 2 to 3 year delay in first breeding (Skutch 1953, Lack 1968). This delay may in part result from lower foraging efficiency by immature cormorants. However, no study of comparative foraging efficiency between cormorant age groups has been previously published.

Our study was initiated to determine relationships of age and foraging abilities in Olivaceous Cormorants (*Phalacrocorax olivaceus*; unless otherwise noted, all references to cormorants mean this species). We used 2 study sites to assess the effect of varying habitat characteristics on cormorant foraging abilities, and to determine if relative age group efficiency rates were similar between different habitats. Differences in relative foraging efficiency and diving abilities of adult and immature cormorants could affect survival rates, and on a broader scale, help explain the development of delayed maturity.

METHODS

Adult and immature (first-year) Olivaceous Cormorants are readily distinguished by plumage differences (Oberholser 1974). Both age groups spent the majority of a day on or adjacent to feeding grounds, using posts, pilings, and trees as perch sites between feeding sequences. We recorded the diving and surface pause times between dives, number of successful dives, duration of feeding sequence, water depth, and weather parameters (e.g., air temp., wind speed, precipitation) for each feeding observation. Either a coworker recorded these activities immediately or we tape-recorded and later timed and transcribed the recordings. All observations were made using 20–45× spotting scopes and/or 7× binoculars from a parked vehicle. A successful dive was scored only when a bird surfaced with and swallowed a prey item (neither size nor species could be accurately determined). Although subsurface prey swallowing does not normally occur (Ross 1976), we assumed that any such activity occurred equally between age groups. Data analysis did not include any sequence of fewer than 10 dives, or one in which a bird was disturbed (e.g., other birds, aircraft, people).

On 10 occasions (5 each) between 19 June and 4 November 1976, we recorded data at 1 of 2 study sites of marked habitat differences. Spoitsman's Road Marsh (SRM), Galveston Island, Texas, was an estuarine area characterized by shallow (0.25 to 0.75 m), tidally influenced water levels. Low tide produced ponds of various sizes that trapped and concentrated prey. Clumps of *Spartina* were scattered throughout the area. Herons, egrets, and other marsh and shore birds also used SRM for feeding. In contrast, Cedar Bayou Spillway (CBS), near Baytown, Texas, was an approximately 50 ha power plant cooling pond. Water levels were held roughly constant and were consistently deeper (0.75 to 2.0 m) than water levels at SRM. The feeding area contained no emergent vegetation. Only several species of terns and gulls fed in the area with the cormorants. Adult and immature cormorants fed in the same areas within each site.

Average percent successful dives (% success), success rates (success/min), diving rates (dives/min), dive times, surface time between dives (pause time), and dive/pause ratios (D/P) were calculated for adults and immatures at each study site. Due to skewed distribution and presence of zero values, we normalized percent data ($\sqrt{x + \frac{1}{2}}$ transformation) following Steel and Torrie (1960) before analysis. Means of adult and immature foraging success and diving times were tested for significant inter- and intra-area differences using Student's t-test. Simple linear correlation coefficients (r) were run for all success and diving variable calculations versus climatic variables, water depth, and time and date of occurrence. The Spearman Rank Coefficient (r_s) was used to determine the relationship between adult and immature success rates.

RESULTS AND DISCUSSION

Adult vs immature foraging efficiency.—Foraging success of adult cormorants was significantly higher than that of immatures; this difference was approximately the same between study sites (Table 1). Foraging techniques of cormorants are thus skills which must be developed through experience.

Immatures had apparently not acquired the foraging ability of adults as they entered their first winter as no increase in their relative efficiency was noted (Fig. 1). An influx of fledglings at various times into study populations may have partially masked minor efficiency gains by first young of the year. However, as most Texas cormorant colonies become inactive by July, the latter 4 months of this study were free of such new additions (as reflected in the last 5 data points on Fig. 1).

Although the relationship was weak ($r_s = 0.310$, t = n.s.), respective success rates of both age groups fluctuated in about the same degree between study dates. We noted no diurnal variation in success or frequency for either age group. Except for one occasion, as adult success increased or de-

TABLE 1

INTER- AND INTRA-AREA COMPARISONS OF ADULT (AD) AND IMMATURE (IMM) OLIVACEOUS CORMORANT FORAGING PARAMETERS

	Cedar Bayou (CBS)		Sportsman's Road (SRM)	
	IMM	AD	IMM	AD
Success (%)	9.9*	17.7*	12.1*	18.5*
Success/Min	0.28*	0.55*	0.92	1.19
Dives/Min	2.76	2.84	6.60	6.21
Diving Time (Sec)	17.82	15.25	6.00	6.50
Pause Time (Sec)	5.49	5.48	3.11	2.89
Dive Pause (D/P)	3.31	2.74	2.04	2.39
Sample Size				
No. Dives	338	435	949	399
No. Birds	25	32	19	14

* $p < 0.05$; all inter-area comparisons, except % success and D/P, were significant ($p < .01$).

creased, immature success did likewise. A factor, or group of factors, may have affected foraging ability of both age groups similarly. All measured weather factors were relatively constant throughout this study, and did not correlate with any diving or success variable. Variations in prey availability

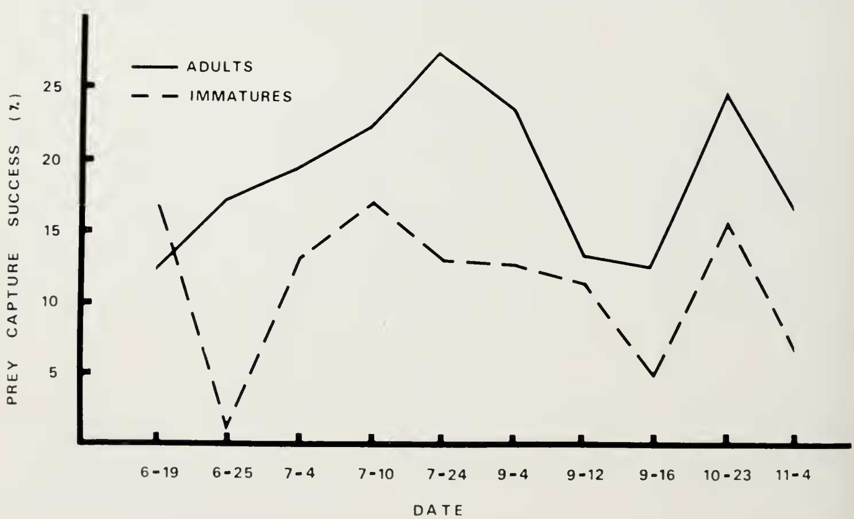

FIG. 1. Comparison of prey capture success (%) of adult and immature Olivaceous Cormorants (results from both study sites combined).

TABLE 2

COMPARISON OF TIME SPENT FEEDING AND TIME BETWEEN A FEEDING SEQUENCE (RESTING) FOR ADULT AND IMMATURE OLIVACEOUS CORMORANTS AT SPORTSMAN'S ROAD MARSH.

	Adults	Immatures
RESTING (MIN)		
$\bar{x}$	92.00*	47.32*
STD. DEV.	51.89	25.11
n	15	19
FEEDING (MIN)		
$\bar{x}$	17.22	20.56
STD. DEV.	8.44	7.85
n	9	16

* $.01 < p < .001$.

among study dates may have affected cormorant success. Dunn (1972) attributed a similar success rate pattern between adult and immature Sandwich Terns to variations in prey availability. Unfortunately, prey species and concentrations were not sampled during this study.

Immatures spent a greater proportion of a day feeding than adults. Although actual time spent in a single feeding sequence did not vary significantly, immatures returned to feed nearly twice as often as did adults (Table 2, data from SRM only; use of scattered roost sites allowed determination of an individual's sequential activities at SRM, while use of a common roosting area prevented following an individual at CBS). Therefore, actual food intake per day may be roughly equal for both age groups. Under this assumption, immatures could obtain adequate food for maintenance provided weather conditions permitted an increase in foraging time as needed. This possibility was suggested for immature Little Blue Herons (Recher and Recher 1969) and Sandwich Terns (Dunn 1972) as a means of compensation for lower capture success.

Rate of adult prey capture (success/min) during a feeding sequence exceeded that of immatures at both study sites, though significantly so only at CBS (Table 1). The deeper, more open water at CBS may have accentuated immature inefficiency. Although not quantified, handling time (manipulation of prey prior to swallowing) and loss of captured prey appeared greater for immatures, further decreasing success (and thus, food intake). Success rate also followed the pattern as shown in Fig. 1.

Although their capture efficiency was lower, immatures have acquired the diving abilities of adults at, or soon after, fledging. Intra-area comparisons of all diving variables were nearly identical for both age groups (Table 1). This suggests that immature foraging inefficiency was caused by a lack of subsurface abilities. The methods by which cormorants pursue, capture, and manipulate prey, along with the musculature associated with feeding, have been studied for adult Double-crested Cormorants (*Phalacrocorax auritus*) by Owre (1967). He felt that vigorous paddling of the feet and steering with the tail were necessary to overcome the difficulties of submerged swimming. Capture technique, maneuverability, and development of a prey search image may thus be gained through experience, and help account for greater foraging efficiency by adults.

Dive/pause (D/P) ratios have been used as an indicator of a species physiological diving abilities (Dow 1964). Similar D/P values for adults and immatures within and between sites is a further indication that both age groups possessed similar diving abilities. If dives and pauses of cormorants are interrelated, then this ratio should remain roughly constant for the species under normal conditions. D/P ratios for several cormorant species were determined (Table 3). Stonehouse (1967) felt that the mean D/P ratio may represent diving efficiency at the family level, while a high ratio for individuals probably represents physiological strain. He concluded that by working well within their physiological limit, cormorants may avoid exhaustion during prolonged fishing spells. Similarities in D/P ratios between various habitats and water depths suggest that the optimum diving rhythm among cormorant species is similar.

Habitat characteristics and foraging abilities.—Variations in habitat characteristics apparently accounted for marked diving rate differences between study sites (Table 1). The approximate 1 m average water depth difference between study sites was an important factor in cormorant diving ability. Significant correlations existed between water depth and all success and diving variables except % success (which does not reflect time spent in a feeding sequence; Table 4). Underwater visibility, substrate configuration, and water quality are other characteristics that vary among habitats and could also affect foraging abilities.

A further indication of inter-area success differences are number and length of daily foraging sequences. These variables were only measured at SRM (as previously discussed; see Table 2), but an indirect comparison between sites can be made. Capture rates were lower for both age groups at CBS relative to SRM, while % success was maintained between sites. This indicated that cormorants increased foraging time at CBS to compensate for lower capture rates. Water levels remained constant at CBS, while those at SRM were tidally influenced. Fish appeared to become trapped, and thus concentrated into small pools during low tide at SRM. Kushlan (1976)

TABLE 3

DIVE/PAUSE (D/P) RATIO OF 6 CORMORANT SPECIES FROM VARIOUS HABITATS.

Species	No. Dives	Habitat (Depth, m)	Mean Dive (Sec)	Mean Pause (Sec)	D/P	Source
Pelagic Cormorant (*P. pelagicus*)	44	Coastal (1.5–6.1)	45.3	23.2	2.0	Dow 1964
Pelagic Cormorant	20	N.A.	29.1	14.5	2.0	Dow 1964
Shag (*P. aristotelis*)	155	Pelagic (N.A.)	40.0	15.0	2.6	Lumsden & Haddow 1946
Great Cormorant (*P. carbo*)	N.A.	Coastal Shallows (N.A.)	25.0	12.0	2.0	Van Dobben 1952
Great Cormorant	34	Coastal (avg. 10.7)	51.0	13.9	3.7	Ross (in press)
Double-crested Cormorant (*P. auritus*)	86	Coastal (avg. 4.7)	25.1	10.3	2.4	Ross (in press)
Olivaceous Cormorant[1] (*P. olivaceus*)	773	Cooling Pond (.75–2.0)	16.0	5.5	2.9	This Study
Olivaceous Cormorant[1]	1,348	Estuary (.25–.75)	6.3	3.0	2.1	This Study

[1] Adult and immature data combined due to similar results.

TABLE 4

CORRELATION COEFFICIENTS (r) FOR WATER DEPTH VS 5 DIVING AND FORAGING SUCCESS VARIABLES OF OLIVACEOUS CORMORANTS

Water Depth vs	Correlations (r)	
	Immatures	Adults
Dives/Min	–0.6088**	–0.7669**
Success/Min	–0.4005*	–0.4684*
Diving Time	0.6495**	0.6531**
Pause Time	0.5071**	0.4921**
Percent Success	–0.1538	–0.0987

* .001 < p < .01.
** p < .001.

found that the feeding efficiency of wading birds increases as water levels recede and fish become concentrated in remnant pools. It may take less time for cormorants to satisfy nutritional requirements at SRM as compared to CBS due to increased availability of prey as water levels fall.

Mortality and life history strategies.—Lower relative foraging efficiency among immatures may be a widespread occurrence in cormorants, as suggested by similar relative success values between sites in this study. The transition from nestling to independence in species whose food is sometimes hard to come by and whose feeding methods are skilled can be difficult (Ashmole and Tovar 1968). Development of prey capture abilities by immature cormorants is probably a strong selective force that eliminates all but the rapid learners.

It would follow that delayed reproduction in cormorants may be partially due to lack of foraging skills. Reproduction should be timed so that an individual can provide food for itself and young; reproductive rate and individual survival are thus maximized (Lack 1968, Recher and Recher 1969). Lowered physiological conditions and/or increased feeding times of immatures resulting from foraging difficulties could act to retard reproductive maturity until such foraging skills are fully developed. The exact length of delay (be it 2 or 3 years) could then vary depending upon a surviving individual's foraging abilities and localized breeding conditions (e.g., nest site and/or mate competition, weather variables, food supply). These views, as developed for numerous species by Lack (1954, 1966, 1968) and Ashmole (1963), have been widely adopted in explaining delayed maturity in several species whose immatures also exhibited foraging inefficiencies (Orians 1969, Recher and Recher 1969, and others).

SUMMARY

Relative foraging efficiency of adult and immature Olivaceous Cormorants was compared on 2 study sites in Texas. Foraging success of adults was higher than immatures, a difference that continued as immatures entered their first winter. Success for both age groups fluctuated in much the same pattern among study dates, and may have been due to prey availability. Immatures increased daily food intake by returning to feed twice as often as adults. Immatures acquired the diving ability of adults soon after fledging. Lower capture success by immatures may be caused by relatively poor capture techniques, maneuverability, and prey search image. Similarities in dive/pause ratio among cormorant species may be related to similarities in the diving abilities of the group.

Diving rate differences between study sites were likely due to variations in habitat characteristics. Significant correlations existed between water depth and all diving variables except % success. Foraging site selection is important to cormorant hunting success. Foraging time apparently increased to compensate for lower capture rates in areas of poor prey availability.

Immature mortality is likely increased during the transition from fledgling to adulthood due to foraging difficulties. Lowered physiological conditions and/or increased feeding times of immatures resulting from poor feeding success may partially explain delayed attainment of reproductive maturity for several years in cormorants.

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